Cameral membranes, pseudosutures, and other soft tissue imprints in ammonoid shells

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Abstract: Ammonoids occasionally show subtle structures linked with the attachment or contact of the soft body with the shell. Only some of these structures were mineralized and thus are rarely preserved. We describe mainly three different kinds of structures, namely (i) cameral membranes, (ii) muscle imprints (excluding muscle attachment structures) and (iii) blood vessels. Cameral membranes (i) have been discovered only in a small fraction of ammonoid species and are close to the siphuncle or cut off parts of the chambers or separate the chamber volumes vertically. Pseudosutures commonly run subparallel to the normal sutures, although they are fainter. They likely formed during the forward movement of the septal mantle prior to the insertion of a new septum. Drag lines (ii) also developed in the course of this process or may represent imprints of muscle fibers. Blood vessels (iii) also left imprints in ammonoid shells.

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Chapter 4
Cameral Membranes, Pseudosutures, and Other Soft Tissue Imprints in Ammonoid Shells

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4.1 Introduction

An essential aim of ammonoid paleobiology is understanding the growth, locomotion, and mode of life of these animals. Evidence of these processes can be gathered from the remains of soft tissues or their traces preserved inside the shell such as cameral membranes, pseudosutures, and muscle scars, as well as other soft tissue imprints. Although these structures have been recognized for at least 100 years, in the last 15 years many important studies relating to their occurrence, ultrastructure, composition, and probable function have been published. This chapter summarizes previous research and focuses on recent advances in understanding cameral membranes, pseudosutures, drag lines, and soft tissue imprints unrelated to muscle attachment.

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4.2 Cameral Membranes

Cameral membranes (or cameral sheets) are the remains of thin, originally organic structures within the chambers of ammonoids (Fig. 4.1). The term "cameral sheets" is preferred by some in order to avoid the implication of a physiological, cellular membrane, but either term is widely accepted. These structures can be divided into two general types: chamber linings, which coat the internal surfaces of the chambers, and suspended sheets, which are three-dimensional sheets internally attached to the shell at two or more different points (Landman et al. 2006, Polizzotto et al. 2007) or along longer lines. Suspended sheets may occur as siphuncular membranes, which extend between the siphuncle and the septum and/or ventral shell floor; transverse membranes, which extend between different points on the septum; and horizontal sheets, which divide the chamber into dorsal and ventral compartments (Weitschat and Bandel 1991).

4.2.1 Taxonomic Occurrence

Cameral membranes have been described in the ammonoid literature for over a century (John 1909; Grandjean 1910; Schoulga-Nesterenko 1926; Hölder 1952, 1954; Schindewolf 1968; Erben and Reid 1971; Westermann 1971; Bayer 1975; 1977; Bandel and Boletsky 1979; Kulicki 1979; Bandel 1981, 1982; Tanabe et al. 1982; Hagdorn 1983; Grégoire 1984; Henderson 1984; Weitschat 1986; Weitschat and Bandel 1991; Keupp 1992; Checa and Garcia-Ruiz 1996; Kulicki 1996; Tanabe and Landman 1996). The taxonomic occurrence of the membranes reported in these publications is wide, including phylloceratids, lytoceratids, ceratitids and ammonitids. More recently, such membranes have also been found in Paleozoic ammonoids such as goniatites (Polizzotto et al. 2007) and prolecanitids (Mapes et al. 2002, Landman et al. 2006) as well as in Cretaceous scaphitids (Polizzotto and Landman 2010). Schoulga-Nesterenko (1926) reported cameral membranes in the goniatite *Agathiceras uralicum* but may have misidentified the specimen (see Polizzotto et al. 2007).

Early work most often described cameral sheets associated with the siphuncle. Weitschat and Bandel (1991) described the most intricate and extensive cameral membranes reported up to that time (Fig. 4.1), including transverse and horizontal

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Ladinian. Berlichingen (Germany), note the membranes on both sides of the siphuncle. **b** *C.* cf. *sublaevigatus*, Künzelsau, Garnberg (Germany), 0–7 m above Cycloidesbank gamma, Ladinian, membranes on both sides of the siphuncle. **c** *C.* cf. *sublaevigatus*, Nitzenhausen (Germany), 70 cm below Tonsteinhorizont 4 (delta), Ladinian, membranes on both sides of the siphuncle. **d** *C.* cf. *sublaevigatus*. Nitzenhausen (Germany), between Tonsteinhorizont 3 and 4 (γ and δ), Ladinian, phosphatized membranes on both sides of the siphuncle. **e** *C.* cf. *evolutus subspinosus*, Heming (France), evolutus Zone, Ladinian, phosphatized siphuncle. **f** *Bukkenites* sp., 104, Dienerian, Amb, Spiti valley, India, membranes on both sides of the siphuncle. **g** Gen. et sp. indet., 104, Amb, Spiti valley, India. **h** *Ambites* sp., Nam 53–20, Dienerian, Nammal (Pakistan), membranes crossing the saddles (separating fillings that differ in color). **i**, **j** horizontal lamellae in *Aristoptychites kolymensis*, Late Ladinian, Barentsøya Formation, Bertylryggen, Spitsbergen. **i** detail. **j** note the protoconch and the absence of horizontal sheets in the first whorls

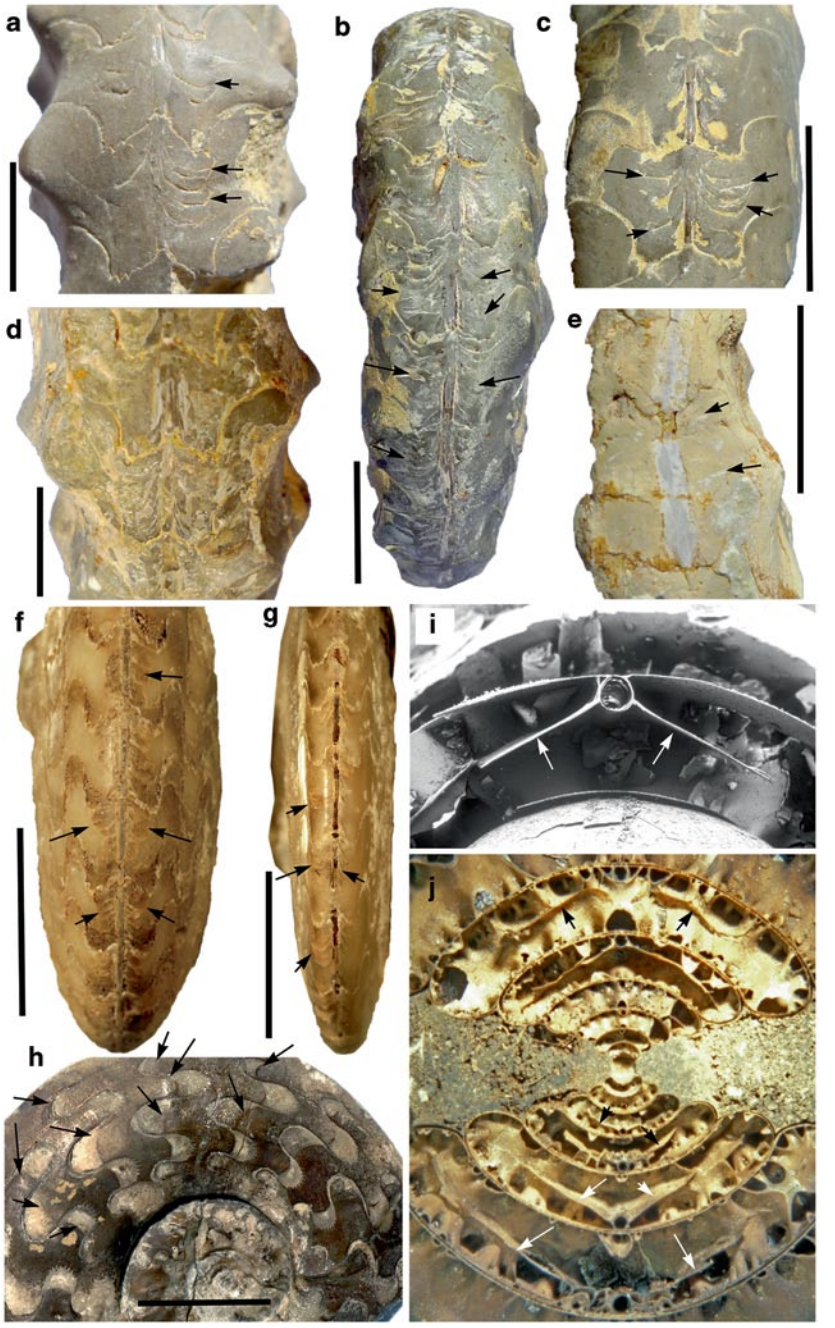

Fig. 4.1 Siphuncular sheets and cameral membranes/intracameral lamellae in various Triassic ammonites; images **a–e** courtesy of H. Hagdorn (Ingelfingen), **g–i** courtesy of D. Ware (Zürich), **j** and **k** courtesy of W. Weitschat (Hamburg). **a** *Ceratites* cf. *münsteri*, postspinosus to enodis-Zone,

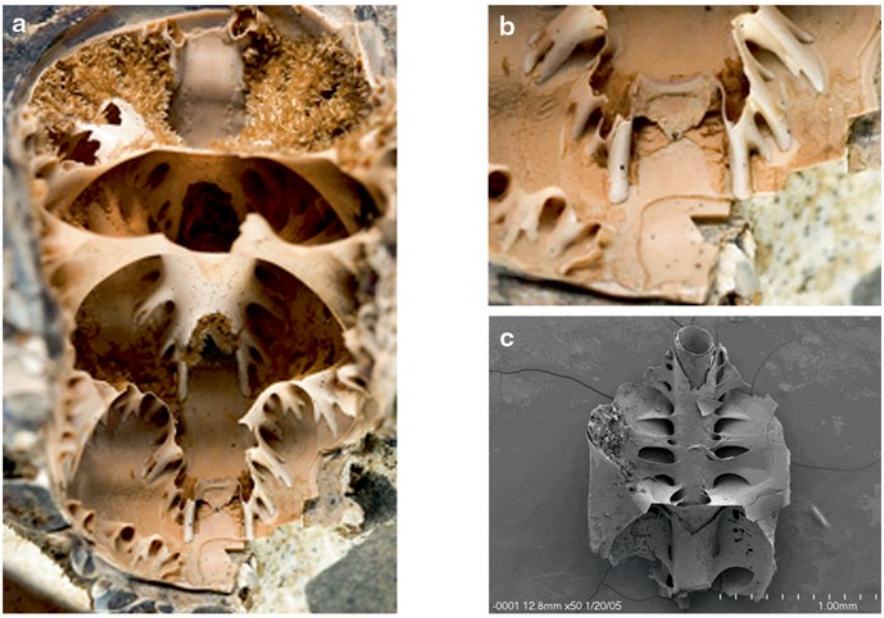

Fig. 4.2 **a** Hollow chambers from a Late Cretaceous *Rhaeboceras halli* from Montana, USA (modified from Polizzotto and Landman 2010). **b** A closer view of the siphuncular sheets and pseudosutures from the specimen shown in **a**. **c** Siphuncular sheets in a Permian *Akmilleria electraensis* from Nevada, USA

membranes in addition to siphuncular membranes. Since that time, transverse and siphuncular membranes have been described in several other ammonoids as mentioned above, but to our knowledge, no other instances of horizontal membranes have been reported. Brief summaries of the earlier descriptions of cameral membranes can be found in Kulicki (1996) as well as Checa and Garcia-Ruiz (1996), and detailed descriptions and images of more recent discoveries (Fig. 4.2) have been produced by Tanabe et al. (2005), Landman et al. (2006), Polizzotto et al. (2007), and Polizzotto and Landman (2010). These studies clarified aspects of the structure, composition, origin, and probable function of the cameral membranes, as discussed below.

4.2.2 Structure and Composition

The ultrastructure of the membranes has been described as thin (< 0.2 μm) conchiolin fibers with no consistent orientation (Tanabe et al. 1982; Grégoire 1987). The chamber linings in particular have been compared to the pellicle in *Nautilus* and *Spirula*, but Kulicki (1996) pointed out that the fibers of ammonoid cameral

membranes are considerably finer. Polizzotto and Landman (2010) described a well-preserved Late Cretaceous scaphite (*Rhaeboceras halli*) in which siphuncular membranes and chamber linings (as well as pseudosutures) were present in the same chamber. Membranes and chamber linings are 1–2 μm thick and composed of irregular globular particles. This is in contrast to the composition reported by Kulicki (1996), but may be more similar to the organic layer secreted on the inner chamber surface in *Nautilus* (Mutvei 1963). Study of the membranes in prolecanitids confirms phosphatic composition (Tanabe et al. 2000). Energy dispersive spectroscopy (EDS) on the *Rhaeboceras* specimen indicated high phosphorus content in the membranes and chamber linings, suggesting an organic origin (Polizzotto and Landman 2010). This hypothesis is accepted by most researchers; however, there is a difference of opinion as to the mode of formation of such membranes (see also the discussion on intracameral deposits in Seuss et al. 2012).

4.2.3 Formation

Two models have been proposed for the formation of cameral membranes. The first proposes that cameral membranes were secreted by the rear mantle as the animal moved forward during chamber formation, and that the shape of the membranes replicates the shape of the rear mantle (the secretion model; Weitschat and Bandel 1991). The second model contends that the membranes are simply the desiccated remains of a hydrogel formed by cameral fluid enriched with organic molecules and shaped by surface tension (the desiccation model; Hewitt et al. 1991; Westermann 1992; Checa 1996). Landman et al. (2006) argued that siphuncular membranes (Fig. 4.2 and 4.4) are not solely the result of cameral liquid dehydration, based on the absence of membranes from early whorls and a consistent first appearance at the end of the neanic stage of ontogeny, as well as the presence of membranes in body chambers in some ammonoids (Polizzotto et al. 2007). The formation of chamber linings is less clear, but the similarity in ultrastructure between chamber linings and siphuncular membranes suggests a similar origin, at least in scaphitids (Polizzotto and Landman 2010). Evidence for the morphogenesis of transverse membranes has not been investigated, and their overall morphology does not immediately rule out either the secretion or the desiccation hypothesis. An examination of the ultrastructure and ontogenetic pattern of occurrence of transverse membranes may shed light on this issue.

In summary, the secretion hypothesis is well supported for the formation of siphuncular membranes in at least some groups of ammonoids (prolecanitids, goniatites, phylloceratids, and scaphitids). There is also some evidence for the secretion hypothesis for chamber linings in scaphitids. Cameral membranes in other ammonoid groups, as well as transverse membranes in all ammonoids, may have been formed either by secretion, desiccation, or a combination of both processes (Checa and Garcia-Ruiz 1996).

4.2.4 Function

Researchers have long proposed that cameral membranes functioned in absorbing cameral fluid, either for fluid transport or for maintenance of a fluid reservoir (Mutvei 1967; Kulicki 1979; Kulicki and Mutvei 1988; Ward 1987; Weitschat and Bandel 1991; Kulicki 1996; Kröger 2002; Landman et al. 2006). This process may have helped in decoupling fluid reservoirs, which may have conferred some physiological benefit. Some researchers have tested a model demonstrating that the presence of cameral membranes may have maintained a reservoir that aided in buoyancy control by rapid fluid re-filling following sublethal shell loss from injury (Daniel et al. 1997; Kröger 2002). Kröger (2002) found that ammonoids survived shell loss up to four times greater than in *Nautilus*, suggesting some sort of buoyancy compensation mechanism. The evidence from Kröger (2002) clearly indicates that a high volume of cameral membranes (up to 14 % of the chamber volume; Hewitt and Westermann 1996) would have made a significant difference in rapidly compensating for shell loss due to injury. Whether or not most ammonoids possessed such a volume of cameral membranes is not yet known.

The capillary action of cameral membranes may also have aided in fluid transport, resulting in faster chamber emptying and thus faster growth rates in ammonoids that formed such membranes. Kröger (2002) suggests that this may be one explanation for increasingly more complex septa during the course of ammonoid evolution, which would have added to the volume of liquid reserved in correspondingly more complex and extensive cameral membranes.

Here, we suggest an additional possible function: the cameral membranes subdivided the chamber volume into smaller volumes. Taking the potentially large amount of chamber water (up to 30 % of phragmocone volume; Heptonstall 1970; Mutvei and Reyment 1973; Reyment 1973; Ward 1979; 1987; Tajika et al. 2014) in the phragmocone into account, water movement might have altered the orientation of the shell *syn vivo*. Cameral membranes would have limited the water movement within the phragmocone chambers and thus enhanced stability. However, the possible effect of moving chamber water needs to be modeled in order to test the potential physical effect of chamber water movements.

4.3 Pseudosutures and Drag Lines

Pseudosutures are incomplete replicas of the suture that are often preserved as raised ridges on the internal surface of the chamber or as lines or etched furrows on the surface of the steinkern between the sutures themselves (Fig. 4.3). Pseudosutures should not be confused with phantom sutures (Seilacher 1968, 1988), which formed when the ammonoid's surface was corroded by a pressurized solution and a phantom of the suture was copied on a lower level of the internal mould. Pseudosutures often occur in series and have sometimes been interpreted as the margins of

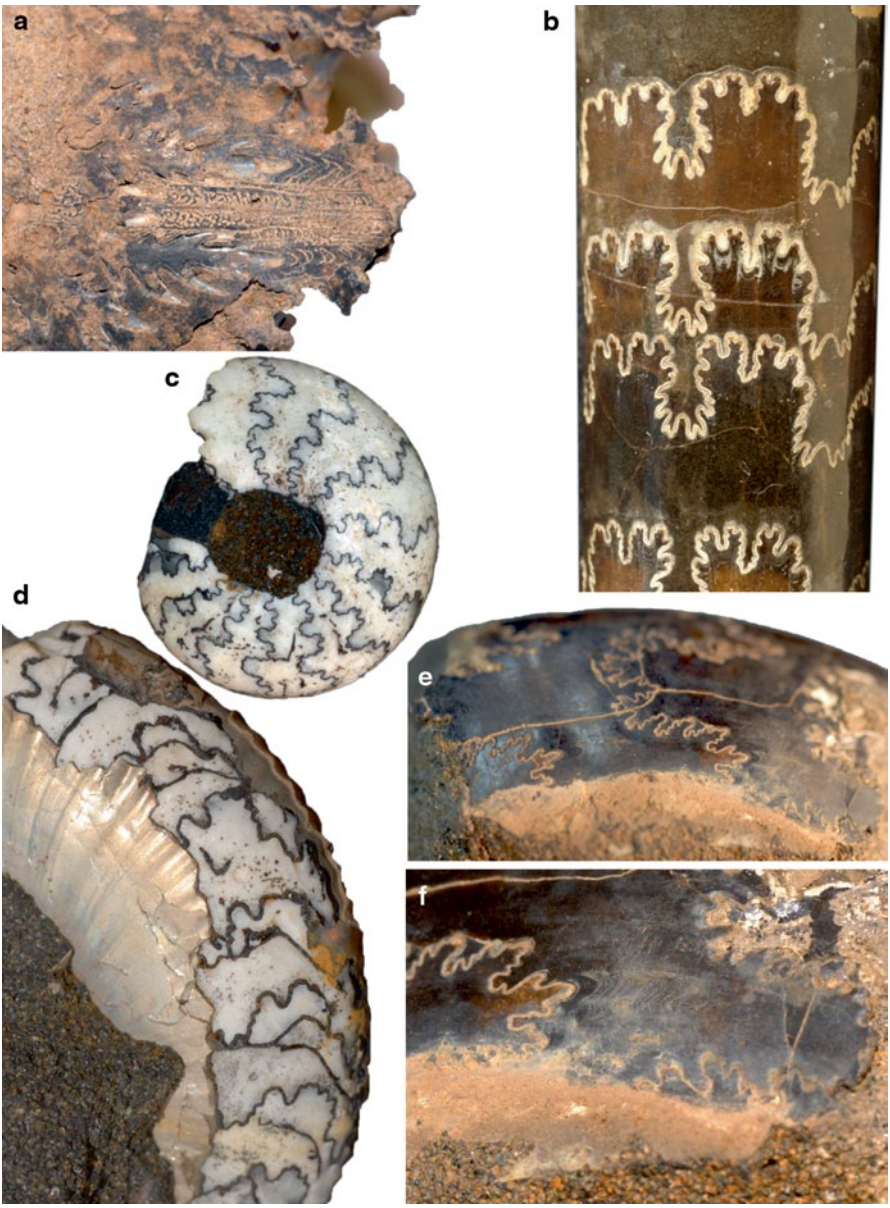

Fig. 4.3 Pseudosutures in various Jurassic and Cretaceous ammonites: **a** *Cadoceras* sp., Callovium, Kostroma Region, Russia, whorl height 12 mm, image courtesy of R. Hoffmann (Bochum). **b** *Baculites mariasensis* with multiple pseudosutures and drag lines associated with all four sutures in the image. Pseudosutures are found near the adapical side of the lobules of each suture. Adoral direction is to the right. **c–f**, *Craspedites* sp., Craspedites nodiger Zone, Cretaceous, Kostroma Region, Russia, images courtesy of R. Hoffmann (Bochum). **c** dm 24 mm. **d**, dm 34 mm. **e, f** image width at top 25 mm

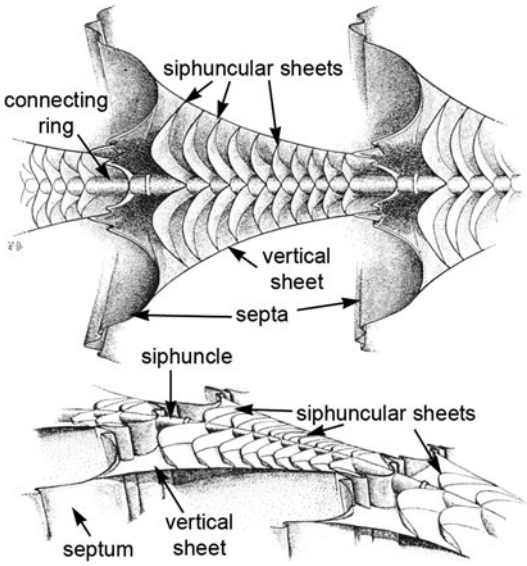

Fig. 4.4 Reconstruction of the siphuncular sheets and the vertical sheet in the Triassic ammonoid *Anagymnotoceras* from Spitsbergen, modified after Weitschat and Bandel (1991)

pseudosepta (Hewitt et al. 1991). The replicated portion may be lobes, saddles, or both, although pseudosutures mimicking lobes appear to be slightly more common. The pseudosutures may be evenly spaced throughout the chamber between sutures (Zaborski 1986), or they may occur singly or in a cluster on one side approaching the lobe or saddle. Pseudosutures most frequently appear on the flanks or ventrolateral portion of the chamber.

Drag lines (or drag bands), which are often associated with pseudosutures, are spiral markings that often (but not always) extend throughout the chamber from lobule to lobule. Like pseudosutures, drag lines form ridges on the internal chamber surface, or their imprints occur as grooves in the surface of the steinkern. In well-preserved specimens, the drag lines extend in pairs from the flanks of the lobe or lobules (Zaborski 1986; Hewitt et al. 1991; Polizzotto and Landman 2010).

4.3.1 Taxonomic Occurrence

Pseudosutures have been described and discussed in numerous ammonoid groups (John 1909; Hölder 1954; Vogel 1959; Schindewolf 1968; Bayer 1977; Hagadorn and Mundlos 1983; Zaborski 1986; Seilacher 1988; Hewitt et al. 1991; Weitschat and Bandel 1991, 1992; Westermann 1992; Landman et al. 1993; Lominadze et al. 1993; Bucher et al. 1996; Checa 1996; Checa and Garcis-Ruiz 1996; Doguzhaeva and Mutvei 1996; Tanabe et al. 1998; Keupp 2000; Richter 2002; Richter and Fischer 2002; Klug et al. 2007; Polizzotto et al. 2007; Klug et al. 2008; Polizzotto 2010; Polizzotto and Landman 2010). The groups in which pseudosutures have been most widely reported include ceratitids, lytoceratids, phylloceratids, perisphinctids, vascoceratids, scaphitids, and goniatitids, but they are found fairly often and probably

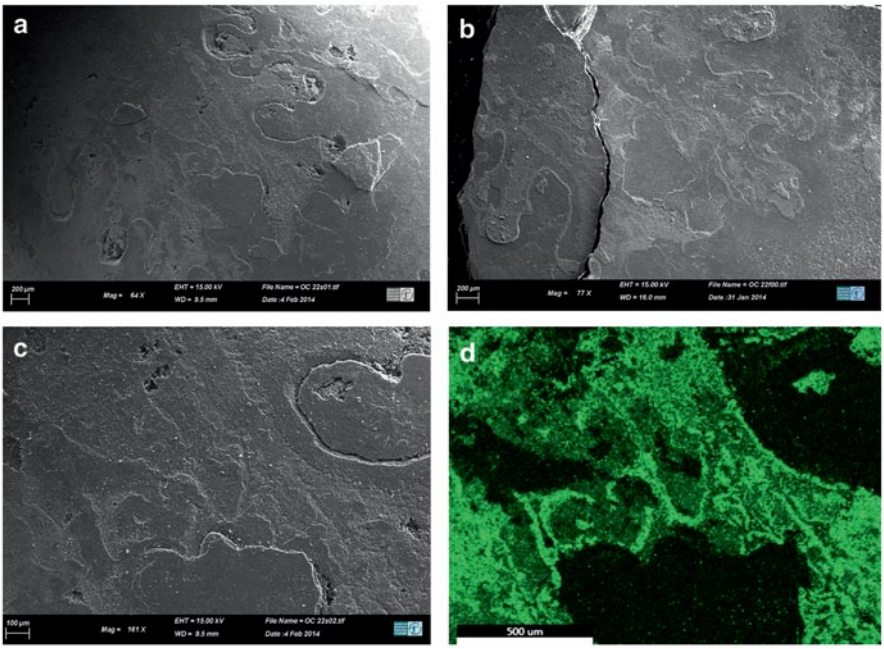

Fig. 4.5 *Eubaculites latecarinatus* from the Late Cretaceous Owl Creek Formation, Mississippi, USA. The upper left image (**a**) is the mould, and the upper right image (**b**) is the corresponding shell fragment. Each image shows the suture line, as well as associated pseudosutures. The lower left image (**c**) is a closer view of some of the suture and pseudosutures on the mould. EDS analysis indicates phosphorus enrichment in the pseudosutures and chamber surface (**d**), but no phosphorus is present on the inner surface of the shell (see text for explanation)

occur to one degree or another in most ammonoid groups. Pseudosutures have also been noted in baculitids (Fig. 4.3b and 4.5, W.A. Cobban unpublished observations, Polizzotto 2010). Drag lines are often reported together with pseudosutures (Fig. 4.1b, c, 4.2, Zaborski 1986; Lominadze et al. 1993; Richter 2002; Klug et al. 2007, 2008; Polizzotto and Landman 2010).

4.3.2 Structure and Composition

Pseudosutures form ridges on the internal surface of the shell, but the imprints (furrows or grooves) of these ridges on the surface of the steinkern are also called pseudosutures. The height and width of the ridges vary, with some pseudosutures quite prominent (20 µm wide and 25 µm high; see Polizzotto et al. 2007), and others less so (2 µm wide and 10 µm high; see Polizzotto and Landman 2010). Drag lines, while oriented differently than pseudosutures (parallel to the direction of growth rather than parallel to sutures; Richter 2002), appear to have a similar morphology in width and height (Polizzotto and Landman 2010).

The original composition of pseudosutures and drag lines is still unclear. Polizzotto et al. (2007) figured various goniatitid pseudosutures in the same specimen, some of which were made up of regular crystals arranged vertically along an asymmetrical slope (similar to the mural ridge in *Nautilus*), and others with a more random crystal arrangement. The pseudosutures in these goniatites sometimes dissolved when etched in acid, indicating an underlying carbonatic composition. At other times, however, the pseudosutures remained intact following etching, and were assumed in such cases to be coated by a now phosphatic and probably originally organic layer. In support of this idea, the thinner pseudosutures described by Polizzotto and Landman (2010) in a scaphitid were composed of (or perhaps coated with) an irregular, globular substance 1–2 μm thick. EDS analysis of these pseudosutures and of the drag lines in the same chamber revealed a high phosphorus content, corroborating an originally organic composition (at least for the surface of the pseudosutures and drag lines). Recent EDS analysis of well-preserved baculitids also indicated phosphorus enrichment (8–10 weight%) in pseudosutures (Polizzotto 2014). In that study, the shell was carefully removed from the mould, and pseudosutures on the surface of the mould were analyzed (Fig. 4.5). In addition, the imprints of pseudosutures on the inner surface of the corresponding shell fragment were analyzed. It is interesting to note that although phosphorus enrichment was found in the pseudosutures themselves, it was absent in the imprints. This implies that pseudosutures may have been composed of an originally mineralized substance (similar to the shell and septum), and then coated with an organic secretion that likewise coated the entire interior of the chamber (see also Polizzotto et al. 2007 and Polizzotto and Landman 2010). When the shell was removed from the mould, the originally organic coating adhered to the mould, explaining the presence of phosphorus on the mould and its absence on the inner shell surface. Though more evidence is needed in additional taxa, it seems likely that the original composition of pseudosutures and drag lines was carbonatic, with an overlying organic coating. It should be possible to verify this by performing EDS analysis on cross-sections of well-preserved pseudosutures. This hypothesis for the composition of pseudostures leads to the question of how these structures were formed.

4.3.3 Formation

Pseudosutures likely formed as an accumulation of secretions from the rear mantle during pauses in forward movement (Weischat and Bandel 1991; Keupp 2000; Landman et al. 2006; Klug et al. 2007; Polizzotto et al. 2007 and references therein). It has also been proposed that siphuncular membranes and pseudosutures formed by a single process as parts of a continuous structure, and that both siphuncular membranes and pseudosutures are simply the remnants of pseudosepta (originally organic membranes that replicated the entire surface of the rear mantle; Hewitt et al. 1991; Westermann 1992; Checa 1996). These pseudosepta would have formed

by either secretion or desiccation, as outlined earlier. We have described evidence above in favor of the secretion hypothesis for siphuncular membranes, and similar evidence suggests that pseudosutures formed by secretion as well (Polizzotto et al. 2007; Polizzotto and Landman 2010).

In addition, recent research has demonstrated that although siphuncular membranes and pseudosutures formed by a similar process (as accumulations of secreted material in the shape of the rear mantle), they are not parts of a single continuous structure (Polizzotto et al. 2007; Polizzotto and Landman 2010). This was confirmed by examining specimens in which siphuncular membranes and pseudosutures occurred in the same specimen or even in the same chamber, which revealed that differences in ultrastructure, position in the chamber, and spacing argue against the single-origin hypothesis.

If it is the case that pseudosutures are composed of an originally mineralized ridge overlain by an originally organic secretion, then two hypotheses of formation are possible. Either two separate but closely located populations of rear mantle cells produced two different secretions in sequence, or the same population of cells produced two different secretions at various points in the chamber formation cycle. It is difficult to test either hypothesis, but it may be fruitful to identify the specific cells that secrete organic and inorganic components of modern molluscan shells.

Drag lines have always been assumed to mark the progress of the rear mantle during translocation, and similarities to pseudosutures in structure and composition suggest that drag lines represent an accumulation of rear-mantle secretions. In contrast to the portion of the rear mantle that secreted pseudosutures, however, the parts of the mantle that formed drag lines must have remained in continuous contact with the shell wall. Alternatively, Klug et al. (2008) hypothesized that some spirally arranged drag lines might represent impressions of muscle fiber bundles in the posterior mantle (rather than secretions).

4.3.4 Implications for Growth

The shape of the pseudosutures and their probable origin as secretory products of the rear mantle corroborates the hypothesis that they formed during pauses in the forward movement of the animal. Many authors have proposed such an explanation for pseudosutures (e.g., Zaborski 1986; Seilacher 1988; Hewitt et al. 1991; Lominadze et al. 1993; Checa and Garcia-Ruiz 1996; Polizzotto et al. 2007; Polizzotto and Landman 2010). Interpretations differ, however, in what the pseudosutures reveal about the process of translocation. Some suggest that the temporary points of attachment served as critical, possibly genetically determined points that helped to maintain the shape of the rear mantle (and thus the consistent shape of the septum) between septa (Henderson et al. 2002; Polizzotto and Landman 2010). This line of reasoning gives rise to the hypothesis that the pseudosutures represent points of temporary attachment for the rear body during translocation (Klug and Hoffmann 2015). In any animal possessing a chambered shell, growth requires repeated de-

tachment of the body from the shell, yet it is unlikely that the animal would have detached the entire body simultaneously. It is clear that *Nautilus* attaches to the mural ridge prior to septal formation, and it appears likely that extinct nautiloids, bactritoids, early coleoids, and many ammonoids did the same. Given the extremely similar morphology and ultrastructure of at least some ammonoid pseudosutures to the mural ridge (Polizzotto et al. 2007), it is possible that pseudosutures also represent points of temporary attachment, at least in some instances. As the occurrence of pseudosutures at particular points along the suture is remarkably consistent within species, this corresponds well to the tie-point hypothesis of septal morphogenesis, first proposed by Seilacher (1975, 1988).

Some have interpreted drag lines as candidates for these tie points (Zaborski 1986; Seilacher 1988); others, however, point out that the coincidence of drag lines with the flanks of the lobules rather than the tips, and their paired occurrence, suggests that drag lines are more likely fused, telescoped pseudosutures (Hewitt et al. 1991; Checa and Garcia-Ruiz 1996; Klug et al. 2007; Klug and Hoffmann 2015). Polizzotto and Landman (2010) reported several different drag lines in a single chamber, none of which were continuous with the pseudosutures in the same chamber. Additionally, some of the drag lines in this specimen were paired and apparently diverged from a single drag line adapically (Polizzotto and Landman 2010, Fig. 5, 6), while other, single drag lines continued nearly all the way to the lobule before ramifying into a short series of concentric ridges at the base of the lobule (Polizzotto and Landman 2010, Fig. 7). Based on observations from all these different specimens, it may be that drag lines formed in more than one way, but in every case they represent a point at which the rear mantle was in contact with (and possibly attached to) the inner shell wall.

An alternative interpretation of pseudosutures proposes that rather than acting as points of attachment, they may represent accumulations of secreted material at points determined by the interaction of the viscoelastic rear body and the varying pressure of cameral fluid and gas behind the body (Checa and Garcia-Ruiz 1996). The mantle did not necessarily attach at the location of the pseudosutures, but simply paused. This corresponds to the viscous fingering model of septal morphogenesis (Garcia-Ruiz et al. 1990; Garcia-Ruiz and Checa 1993; Checa and Garcia-Ruiz 1996). This model, however, would not explain the evidence of the attachment-like ultrastructure in at least some pseudosutures.

Klug et al. (2008) introduced a "*tension model*" of septal morphogenesis that incorporates elements of both the tie-point model and the viscous fingering model, in which muscle fibers at the edge of the rear mantle attached to the inner shell, and the more complex the shape of the septum, the more tension could develop in the rear mantle and in the organic pre-septum prior to mineralization. While Klug et al. (2008) did not elaborate specifically on the consequences of this model for the formation of pseudosutures, the model implies that the shape of temporary attachment points would have depended on components of translocation that were not so much genetically influenced, but mainly affected by changes in chamber pressurization. For more details on septum formation see Klug and Hoffmann (2015).

In addition to implications for septal morphogenesis, the number, placement, and spacing of pseudosutures may indicate the pace and timing of chamber formation. These interpretations, however, rely on the assumption that pseudosutures were secreted periodically, which is currently not possible to verify. These pauses, if they are such, might also correspond to growth rhythms recorded in growth lines or lirae formed at the aperture; however, this hypothesis has not yet been tested. There does not seem to be any analogous structure or process in *Nautilus* or *Sepia*, leaving us with little to substantiate the periodicity of pseudosuture formation one way or the other. The only similar structure seen in modern nautilids are spiral drag lines, possibly representing imprints of mantle muscle fibers and/or fine arteries in the mantle (Klug et al. 2008).

In summary, it appears plausible that pseudosutures record short pauses in forward movement during the chamber formation cycle, and it is likely that at least some pseudosutures (or pseudosutures in some taxa) represent the imprints of ephemeral soft-tissue attachment. Drag lines do not offer any evidence of the pace of translocation or of pauses, but they do show that at least some parts of the mantle were in continuous contact with the shell wall and may have formed attachment points. Such attachments may have helped to anchor parts of the animal in the body chamber during translocation, as well as helping to maintain the fundamental shape of the rear mantle in between formation of consecutive septa.

4.4 Other Soft Tissue Imprints

Other soft tissue imprints, particularly on the septum, have been recently described in ammonoids by Klug et al. (2008) (Fig. 4.6). These include the septal furrow and associated subparallel furrows (extending from the mid-dorsal suture to the siphuncular perforation); striations on the mural band and on the annular elevation; the conchal furrow on the venter (especially on the body chamber); and deformed septa (non-taphonomic deformities). These specific features had previously been reported only in nautiloids and bactritoids (Klug et al. 2008 and references therein), and were interpreted as the imprints of muscle fibers and blood vessels in the septal mantle. The presence of these features in nautiloids, bactritoids, and early ammonoids (Devonian), and their apparent absence in more derived ammonoids (with the exception of the conchal furrow, which appears in Cretaceous ammonites, Landman and Waage 1993), led Klug et al. (2008) to hypothesize that higher tension in the organic pre-septum due to the higher order septal folding may have prevented imprinting of soft tissue structures (see the summary of Klug et al.'s tension model of septal formation above).

Klug et al. (2007) found a black layer on the dorsal surface of some ammonoid shells (see also Keupp 2000). This layer is presumably originally organic and most likely similar to the black layer found in recent and fossil nautiloids.

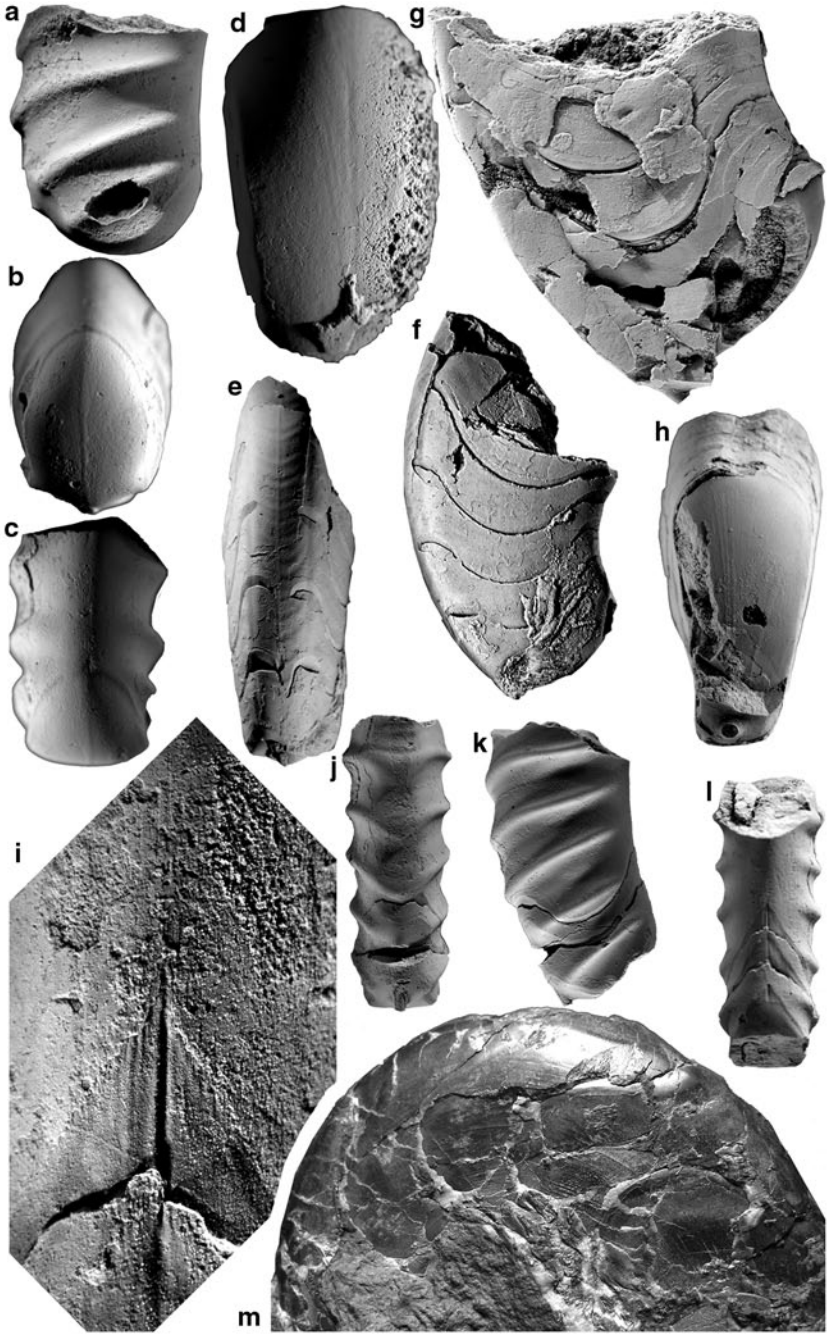

Fig. 4.6 Soft-tissue imprints in the shell and septa of Early Devonian ammonoids, modified after Klug et al. (2008). **a–c**, *Erbenoceras advolvens* (Erben 1960), PIMUZ 7494, early Emsian, Hassi Chebbi, Tafilalt, Morocco, length 13 mm. **a** Septal view to show the septal furrow. **b** Lateral view.

4.4.1 Blood Vessel Imprints

Some septa of the Early and Middle Devonian ammonoids *Chebbites*, *Erbenoceras*, *Gracilites*, *Metabactrites*, *Rherisites*, and *Pinacites* show long wrinkles on the surface (Klug et al. 2008). Some of these wrinkles lie in the plain of symmetry (septal furrow; Stenzel 1964; Teichert 1964; Chirat and von Boletzky 2003) and some diverge from the plain of symmetry at a low angle, originating near the siphuncle (Fig. 4.6). Similar shallow imprints can be seen in modern nautilids: In some *Nautilus* conchs, Klug et al. (2008) found imprints of the left and right septal arteries, the siphuncular artery and the accessory siphuncular arteries (see also Deecke 1913, and Stenzel 1964, who figured a *Nautilus* septum showing soft tissue imprints). Corresponding to this fact, the imprints on the septa of the Devonian ammonoids were interpreted as imprints of arteries, providing the septal mantle with arterial blood. The absence of these structures in more derived ammonoids has been linked with the increase in septal frilling, which might be linked with a higher tension of the organic septum prior to mineralization. Accordingly, the more tightly stayed pre-septum would have prevented the formation of soft-tissue impressions in the septum.

On the inside of the shell wall, both nautiloids and ammonoids of various ages show the conchal furrow ("Fadenkiel" of von Bülow 1918; see also Teichert 1964; Shimanskij 1974; Landman and Waage 1993; Chirat and von Boletzky 2003; Keupp 2012). This furrow can be traced in nautilids from the cicatrix to the aperture, while in ammonoids, no corresponding structure has yet been found on or near the initial chamber. In ammonoids, it is rarely seen but throughout the entire phylogeny of ammonoids from the Early Devonian to the Late Cretaceous (Landman and Waage 1993; Klug et al. 2008). Doguzhaeva and Mutvei (1996) suggested that this midventral longitudinal elevation was the "attachment site for a ligament or a muscle used to maintain the shape and position of the circumsiphonal invagination during the growth and forward migration" of the soft body (Chirat and von Boletzky 2003, p. 168). Griffin (1900, fig. 11) illustrated the "lesser aorta and its branches", including the midventrally running pallial artery. Potentially, it may have been this artery that occasionally left a mid ventral imprint on the inside of the shell of various ectocochleates.

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c *Ventral* view. **d** *Chebbites reisdorfi* Klug (2001), PIMUZ 27000, septal view, early Emsian, Hassi Chebbi, Tafilalt, Morocco; note the septal furrow and additional subparallel furrows on the right; length 15 mm. **e, f,** *Rherisites* sp., PIMUZ 27072, early Emsian, Hassi Chebbi, northern Tafilalt, Morocco; length 16 mm. **e** Ventral view, note the conchal furrow. **f** Lateral view, note the epizoans. G, H, The ammonoid *Gracilites* sp., PIMUZ 27070, early Emsian, Hassi Chebbi, northern Tafilalt, Morocco; length 30 mm. **g** Lateral view, note the pseudosutures. **h** Septal view, note the striations that run subparallel to the plane of symmetry. **i-l**, *Metabactrites ernsti* Klug et al. (2008), PIMUZ 7404, early Emsian, Ouidane Chebbi, Tafilalt, Morocco, length 25 mm. **i** detail of note the septal furrow, the striation on the mural part of the septum and the striation in the body chamber (probably within the attachment site of the dorsal muscle); height of detail 1.6 mm. **j** Ventral view. **k** Lateral view. **l** Dorsal view. **m** Agoniatitida gen. et sp. indet., MB.C.0782, late Emsian, Wissenbach Slate, Wissenbach, Germany

4.4.1.1 Muscle Imprints

Similar to the above mentioned arteries, bundles of muscle fibers in the posterior mantle might have left imprints on the septum as well as on the inside of the outer shell, as noted in some Devonian ammonoids (Klug et al. 2008). This can also be seen in nautilids (Deecke 1913; Stenzel 1964), where the orientation of some imprints coincides with the orientation of muscle fibers in the septal mantle (Klug et al. 2008). In agreement with the findings in modern nautilids, both the spirally arranged drag lines on the inside of the shell and the radially arranged impressions on the margin of the septum on its mural part (Fig. 4.6i) were interpreted as imprints of mantle musculature (Klug et al. 2008). Of course, attachment scars of various larger muscles are occasionally seen in well preserved ammonoid specimens. These structures are described in Doguzhaeva and Mapes (2015).

4.4.1.2 Other Imprints

From a few ammonoid taxa, tension wrinkles have been described (Checa and Garcia-Ruiz 1996; Klug et al. 2007). These wrinkles are one to several micrometers wide and ten to several tens of micrometers long. They are situated at the mural part of the septum. According to Checa and Garcia-Ruiz (1996), these wrinkles document the flexibility of the organic membrane prior to the mineralization of the septum. For an illustration, see Klug and Hoffmann (2015).

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